# Tidal and Seasonal Patterns in the Chondrophore of the Soft-Shell Clam *Mya arenaria*

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*Thin sections of a compact, internal structure projecting
from the hinge region of the bivalve* Mya arenaria *reveal
the presence of tidal and seasonal patterns. This is the first
demonstration that microgrowth increments are formed
in a structure not associated with the growing edge of the
shell. The clarity and simple orientation of these extensive
patterns, combined with the resilience of the hinge region
to disturbance and damage, suggests that detailed ex-
aminations of internal shell structures will prove valuable
in ecological, archaeological, and paleoecological studies.*

Ecologists, archaeologists, and paleoecologists share an
interest in the calcified layers of animals, because such
layers can be preserved and can record growth variations.
The shells of bivalve mollusks consist of two or more
calcified layers that can differ considerably in composition
and structure. These layers are formed by the mantle tissue
in different regions of the shell. The outer layer is deposited
at the ventral or growing margin. The innermost layer
forms in interior regions generally behind the pallial line
(1), a region where the mantle tissue attaches to the shell.
As one might expect, growth patterns within the shell are
also preserved to a different degree in these layers. Several
investigators have suggested that the finest, most detailed
growth records are formed in the outer layer, while only
major patterns in growth can be resolved in the innermost
layer (2, 3). Experience to date has borne this out. Daily
and tidally produced growth increments have been doc-
umented in the outer shell layer of a variety of species (2,
4–7). Only annual and seasonal patterns have been iden-
tified in the inner shell layer (3, 8–13).

Here we report, for the first time, the presence of tidally
deposited growth increments within an inner shell layer

and within a structure associated with the hinge region
rather than the ventral margin of the shell. We also de-
scribe the occurrence of well-defined seasonal patterns in
this species and suggest that, when present, detailed mi-
crogrowth records in the inner shell layer may more ac-
curately reflect the physiological state of a bivalve than
comparable patterns within the outer layer. The species
studied is the soft-shell clam, *Mya arenaria*, which is
widely distributed along the coastal areas of the North
Atlantic and North Pacific Oceans.

Searching for growth patterns in the inner shell layer
is not a common procedure, but tends to occur only after
it has been determined that growth patterns are for some
reason poorly preserved in the outer layer of the species
being studied (13). This is the case for *Mya arenaria*. The
shell of this species is thin and always shows signs of con-
siderable damage, abrasion, and erosion. The ventral
margin is usually chipped, irregular, and frequently re-
paired. Growth records are poorly preserved in cross-sec-
tions of the valve and are unreliable for estimating the
age of individuals (8, 14). Instead, investigators have con-
centrated on examining the chondrophore, an internal,
spoon-shaped shelf projecting from the hinge region of
the left valve (Fig. 1a). Using thin sections or acetate peel
replicas of the chondrophore, several prior studies estab-
lished the presence of annual patterns (8, 14–16), and in
one case (17), the presence of intra-annual features was
noted.

Samples of *Mya arenaria* were collected bimonthly in
1986–87 and monthly during 1988–89 at an intertidal
location in Stony Brook Harbor, Long Island, New York.
Thin sections were produced according to the methods
described in detail by Clark (18), and the shells were pre-
pared as follows. First, the chondrophore, along with a
portion of the left valve, was sectioned from the umbo to
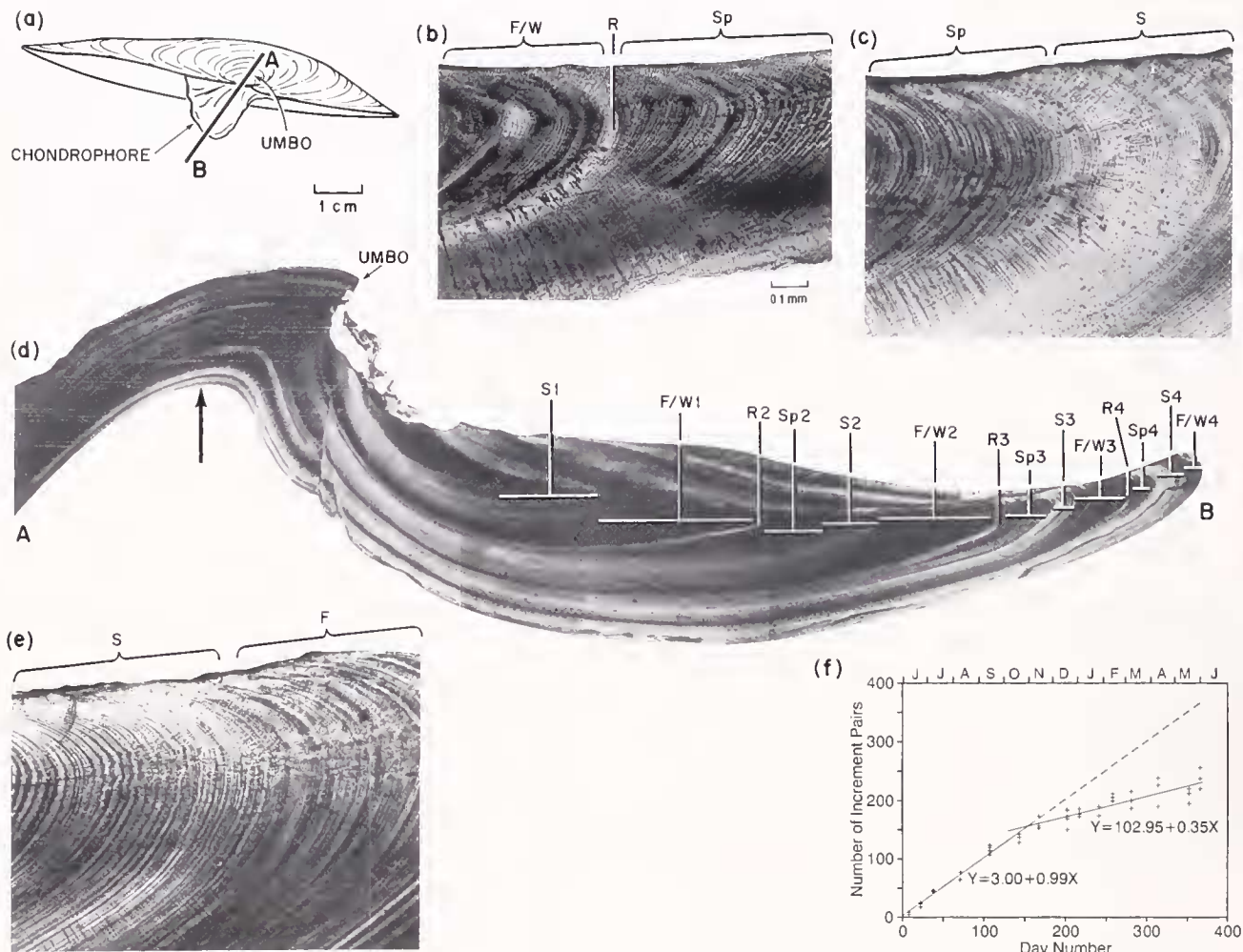
**Figure 1.**   *Microgrowth patterns in the chondrophore of* Mya arenaria. *(a) View of left valve with associated chondrophore. Line A–B shows orientation of thin sections. (b), (c), and (e) Optical micrographs of thin sections illustrating the detailed microgrowth increment patterns. Note the seasonal variations in increment thickness and morphology. All three micrographs to same scale. (d) Composite optical micrograph of a thin section of the chondrophore and hinge region of a 4+ year old individual. Distinct summer (S) and spawning features (R) are evident. Spring (Sp) and fall/winter (F/W) appear as dark (opaque) regions in thin sections. Specimen collected in March 1989. (f) Counts of the number of microgrowth increment pairs occurring after the spawning band versus day number during 1988–89 (n = 46). Based on monthly sampling, the spawning band was produced in individuals after 13 May and prior to 8 June, the first date plotted in the figure. For the regression, 1 June is defined as the origin. The segmented or two-phase linear function was fit by least squares under the assumptions that the location of the join point was unknown and error variances in the two segments were unequal. Detailed methods for this regression may be found in Hudson (30). Slope of the first line segment verifies the semidiurnal rate of increment deposition (95% CI: $0.94 \leq b_1 \leq 1.04$ pairs of increments per day). Rate of increment production decreases in fall/winter as shown by the slope of the second line segment (95% CI: $0.28 \leq b_2 \leq 0.41$ pairs of increments per day).*

the chondrophore edge (Fig. 1a). Specimens were then mounted onto petrographic slides, sectioned a second time, ground, and polished by hand. Thin sections of 231 specimens were examined under transmitted light using a compound microscope at low magnification (12.5–100×). We analyzed growth patterns primarily by characterizing how features present at the edge of the chondrophore changed from one sampling date to the next.

Unless otherwise noted, the specific features described below occurred in 90% or more of the specimens that were examined and that had been properly prepared.

The resolution of growth patterns in the chondrophore depends to a large extent on the thickness of the section (Fig. 2). Distinct variations in transparency are found in thin sections ground to 150–250 microns (Fig. 1d). At some time during May–June of each year, a thin trans-

lucent band is formed at the edge of the chondrophore (Fig. 2b); this event coincides with the spawning season, which was identified by Brousseau (19) for several nearby populations. This translucent band occurs infrequently in one-year-old individuals (32%). It is, however, readily apparent at all other ages up to the oldest individuals examined (91% of specimens 2–5 years old).

The translucent spawning band is followed by a seasonal cycle consisting of an opaque (optically dense) region formed in spring, a broad translucent region in summer, and a second opaque region in fall-winter (Fig. 2a–e). No discernible change differentiating fall from winter is apparent at the edge of the chondrophore, but an opaque layer does begin forming in January on the inner surface of the region where the chondrophore joins with the umbo (large arrow in Fig. 1d). This opaque layer is initially

patchy and thin but increases in size and thickness during the winter.

When sections are ground thinner to 80–150 microns, extensive series of microgrowth increments become evident (Fig. 1b, c, e). These also vary seasonally with broad, regularly shaped increments in spring, grading into closely spaced, regular increments in summer. Regularly shaped increments also tend to be deposited during early fall, but by mid-fall, and throughout the winter, the increments appear irregular in form (e.g., see transition in Fig. 1e). In addition, increment widths may be variable during early fall, but they gradually decrease in thickness during this season and remain thin throughout the winter.

The number of microgrowth increments in the interval between the most recent spawning band and the edge of the chondrophore can be related to the date of sample
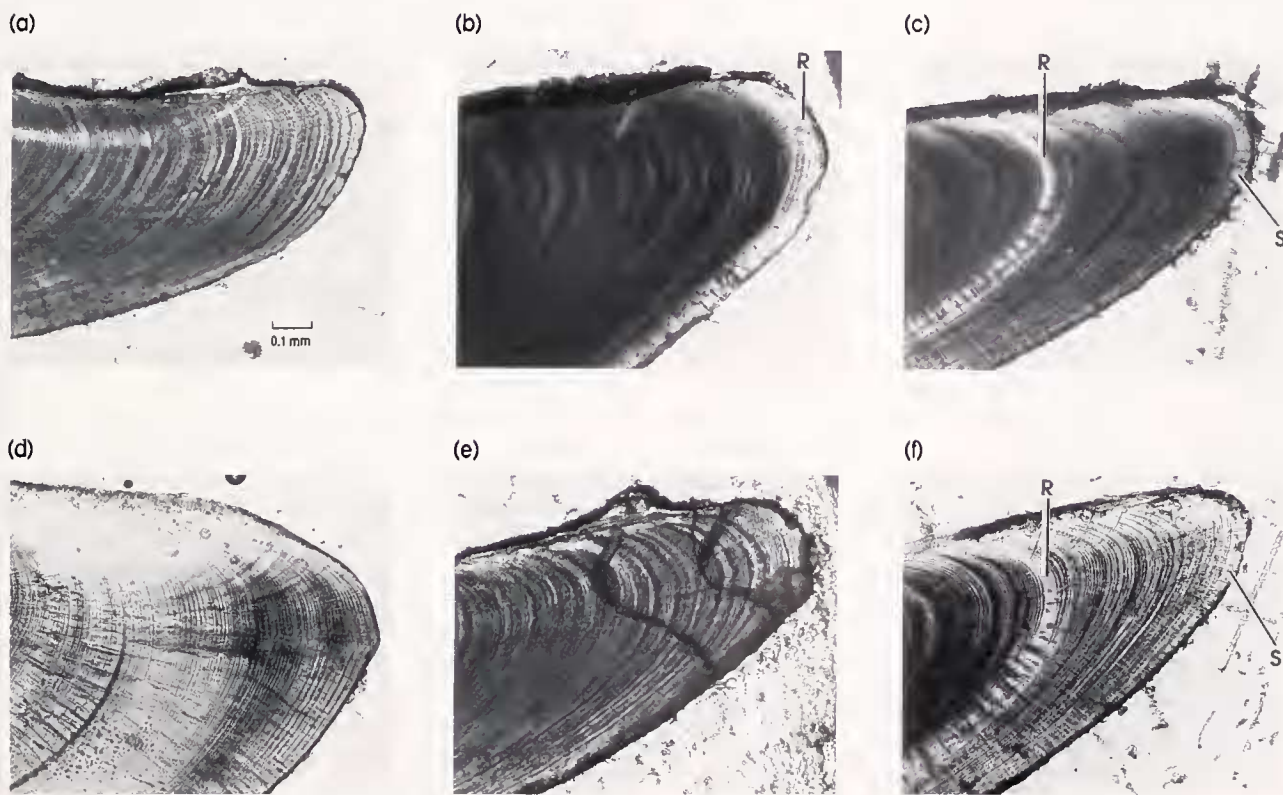


**Figure 2.** Optical micrographs illustrating both seasonal changes at the edge of the chondrophore and the effect of section thickness on the resolution of microgrowth patterns. All micrographs to same scale. (a) Late winter collection. Opaque region with irregular microgrowth increments present at the edge of the chondrophore. Thin section is about 120 microns in thickness. (b) Spring collection. Newly formed spawning band (R) at the edge of the chondrophore. Opaque region in interior is previous winter; 180 micron thin section. (c) Early summer collection. Translucent region characteristic of summer growth (S) is just beginning to form at edge. Note spawning band (R) in interior and opaque spring region (between R and S); 180 micron thin section. (d) Early fall collection. Opaque region forming at edge. Note translucent summer region in interior; 100 micron thin section. (e) Early winter collection. Opaque region with irregular microgrowth increments occurs at edge. Interior region includes previous fall; 120 micron thin section. (f) Same individual as in (c) but with chondrophore ground to about 130 micron thickness. In general, microgrowth increments become evident but the contrast between opaque and translucent regions is lost as the section is ground thinner.

collection (Fig. 1f). Increments are produced at a semi-diurnal tidal frequency during the warmer months (*i.e.*, water temperatures above 15°), when a one-to-one correspondence is found between pairs of increments and day number. By mid-fall, the number of increment pairs produced per day falls below 1.0, but some increment production continues through the winter. We do not know whether this decline is due to a decrease in the rate of increment production, to periods of growth interruption, or to shell dissolution. The decline does, however, coincide with the formation of irregularly shaped microgrowth increments. We have also observed that older, slower growing individuals (4–5 years) tend to form irregular microgrowth increments, even during the warmer months, and increment production in these individuals no longer occurs at a semidiurnal tidal frequency.

Another common feature supports our semidiurnal tidal interpretation: *i.e.*, in portions of the chondrophore of almost every specimen examined, pairs of increments are separated by a diffuse, rather than a distinct boundary and appear coupled (*e.g.*, spring periods in Fig. 1b, c). This type of pattern has been observed in the outer shell layer of other species, and in each instance has been shown to be tidal in origin (2, 4, 7, 20, 21). In these prior studies, investigators have found that the alternating diffuse and sharp boundaries between increments are formed either when the semidiurnal tides are mixed (*i.e.*, unequal) (2, 7, 21) or when they are accompanied by large diurnal temperature variations (4, 20).

While we have demonstrated that detailed tidal patterns occur in the chondrophore, we do not generally expect that a direct correspondence will be found between microgrowth records produced in the inner and outer shell layers of bivalves. Increment deposition at the ventral margin is influenced by a wide variety of environmental conditions, including perturbations due to abrasion during movement, unsuccessful predator attacks, storms, and any other disturbances that may cause local injury or withdrawal of the mantle tissue (22). On the other hand, the inner shell layer, and the chondrophore in particular, is removed from direct contact with the external environment. The disturbance threshold required to affect increment deposition should be higher, and we expect that only environmental changes that cause a systemic physiological response will tend to be recorded. Thus, microgrowth patterns in the inner shell layer should contain less environmental noise due to minor disturbances and should be more integrated with, and more accurately reflect, the physiological processes of a bivalve than comparable patterns deposited in the outer shell layer.

Supporting this view is the sharp contrast between the distorted, highly disturbed form of the outer shell layer in *Mya arenaria* and the detailed, and at times very uniform, patterns preserved in the chondrophore. Another

indication is the prominence of features in the chondrophore associated with the two periods of greatest physiological stress for *Mya arenaria, i.e.*, summer and spawning. The soft-shell clam is a boreal species, and summer represents an extended period of energetic stress due to high water temperatures and potentially low food supplies on Long Island's tidal flats. During July and August, water temperatures in protected, intertidal areas consistently reach 26–28° (23), and chlorophyll-a concentrations in both the water (24) and surficial sediments (23) can undergo mid-summer declines. Kennedy and Mihursky (25) have shown that the metabolic requirements of *Mya* continue to increase with temperature up to 30° and have suggested that high temperatures can lead to starvation if food supplies are scarce. Above 30°, *Mya* suffer significant mortalities (26). In *Mercenaria mercenaria*, the occurrence of a similar translucent region in the middle shell layer has been termed a "stress zone" by Clark (27) and has been observed to form when water temperatures exceed 25° (28), the upper limit for optimal shell growth in this species (29).

The second stress period, associated with spawning, appears as a prominent translucent band consisting of four or more closely spaced microgrowth increments (Fig. 1b, 2b, c, f). The morphology of this feature is very similar to the spawning band in the outer shell layer of *Mercenaria mercenaria* (22). However, in *Mercenaria mercenaria*, the spawning band is less prominent than growth interruptions produced by discrete environmental disturbances (22).

The hinge region in bivalves is the most resilient part of the shell, and it is also the only part containing a complete record of growth. These characteristics make the presence of detailed patterns in the hinge region particularly valuable in archaeological and paleoecological applications. For example, we are currently analyzing 1200-year-old, shell-bearing, archaeological deposits in which fully intact specimens of *Mya arenaria* are rare. However, complete chondrophores are commonly recovered, and both seasonal and microgrowth increment patterns are well preserved. These patterns are allowing us to reconstruct detailed aspects of growth in *Mya*, as well as to infer seasonal shellfish-harvesting practices for this species.

Chondrophores, cardinal platforms, and other internal structures associated with the hinge occur in many bivalve taxa but have been overlooked as potential sources of detailed microgrowth increment records. Our observations suggest that the microgrowth records preserved in these structures are not simply reflections of patterns found in other parts of the shell. As in the case of *Mya*, internal structures may contain the only usable growth patterns. At the very least, these patterns should have less environmental noise and should be more closely coupled to systemic physiological processes. Given the clarity and simple

orientation of the microgrowth increments found in the chondrophore, these structures will also be quite amenable to microprobe and image analysis examination.

## Acknowledgments

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